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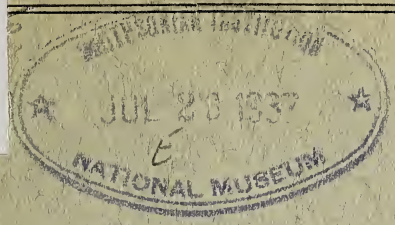

PART 2.

TRANSACTIONS

OF THE

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RICHARDS, O. W., M.A., D.Sc., F.R.E.S. : A Study of the British Species of *Epeolus* Latr. and their Races, with a Key to the Species of *Colletes* (Hymen., Apidae).

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 4. 14TH JULY, 1937. PART 2.

A STUDY OF THE BRITISH SPECIES OF *EPEOLUS* LATR. AND THEIR RACES, WITH A KEY TO THE SPECIES OF *COLLETES* (HYMEN., APIDAE).

By O. W. RICHARDS, M.A., D.Sc., F.R.E.S.

The genus *Epeolus* consists of a number of parasitic bees which attack members of the bee-genus *Colletes* (the subgenus *Triepeolus* is said to attack Anthophorids). The European species have lately been revised by Bischoff (1930, and in Schmiedeknecht, 1930). Bischoff has described several new species which are supposed to be confined to particular hosts. According to his system, English material would be arranged as follows :—

PARASITE.	HOST.
E. productus Thoms.	*C. daviesana* Sm.
E. marginatus Bisch.	*C. marginata* Sm.
E. cruciger (Panz.)	*C. fodiens* (Geoffr. *in* Fourcr.)
var. *similis* Höppn.	*C. succincta* (L.)

The characters (as given by Bischoff) separating the last three forms are extremely slight and there is no indication as to how much material was examined. I have, therefore, thought it worth while, before adopting his system, to examine extensive British material.

In making this study I have been generously aided by a large number of entomologists who have lent me, or given me access to, specimens of *Epeolus* and have supplied habitat data, etc., for the species of *Colletes*. I am glad to have this opportunity of thanking Mr. R. B. Benson (Natural History Museum), Dr. K. G. Blair, Mr. H. Britten (Univ. Museum, Manchester), Prof. G. D. H. Carpenter (Hope Dept., Oxford Univ. Museum), Prof. J. W. Carr, Mr. A. Fergusson, Dr. J. W. Fordham, Mr. P. H. Grimshaw (Royal Scottish Museum), Dr. F. H. Haines, Mr. H. M. Hallett, Mr. A. H. Hamm, Dr. B. M. Hobby, the

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late Mr. H. P. Jones (Public Natural History Mus., Nottingham), Mr. G. J. Kerrich (University Museum, Cambridge), Mr. F. Leney (Castle Museum, Norwich), Mr. C. H. Murray (Free Public Mus., Liverpool), Mr. C. Nicholson, Mr. G. E. J. Nixon, Mr. G. M. Spooner, Dr. R. A. Staig, and Rev. A. Thornley. Finally, I wish to thank Dr. Bischoff for examining one puzzling specimen.

With the aid of these helpers, I have been able to examine 273 ♀♀ and 109 ♂♂ of *E. variegatus* (L.) (=*productus* Thoms.) and 313 ♀♀ and 91 ♂♂ of *E. cruciger* (Pz.) (=*rufipes* Thoms.). In the following records, any locality given without reference to a previous publication is based on specimens which I have examined, or, if accompanied by another entomologist's name, is based on information received in correspondence.

I. The hosts.

(*a*) Separation of Species.

The following key will assist in separating the British species of *Colletes*. The key should be used with some caution. The species will not be found difficult to separate provided some material is available for comparison.

Females.

1. Large species (L. about 13 mm.). Abdomen with whole surface clothed with long hairs, tergites without apical pale pubescent bands. Malar space nearly twice as broad as long ..... *C. cunicularia* (L.).

— Smaller species (L. under 11·5 mm.). Abdomen mainly with very short hairs, with distinct apical pubescent bands ... 2.

2. First abdominal tergite very closely punctured. Tergite 2 with a pale pubescent basal band ..... 3.

— First abdominal tergite relatively sparsely punctured ..... 6.

3. Clypeus with dense procumbent pubescence. (Tergites with apical pubescent bands yellow-tinged. Tergite 1 as densely punctured as possible, dull, apical band interrupted, apical impression black or pitchy, tergite with long hairs arising from its whole anterior face and even from base of dorsal surface. Malar space (fig. 2) 7-8 times as broad as long) ..... *C. fodiens* (Geoffr. *in* Fourcr.).

— Clypeus with less dense pubescence. First tergite less closely punctured, more shining ..... 4.

4. Apex of abdominal tergite 1 testaceous. Malar space (fig. 1) about two and a half times as broad as long. (Pale abdominal pubescent bands yellow-tinged. Base of tergite 1 with long pubescence, which, as it approaches the dorsal surface, becomes dense, short and procumbent. Thorax

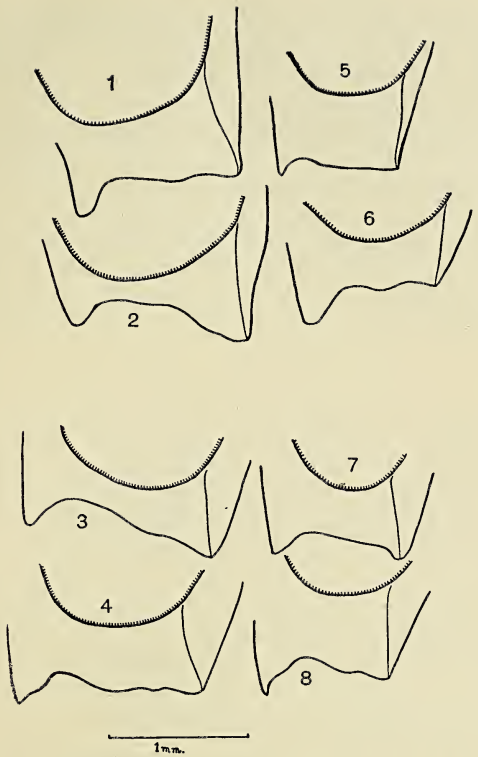

Fig. 1. Left malar space of *Colletes succincta* (L.) ♀.
,, 2. The same of *C. fodiens* (Geoffr. *in* Fourcr.) ♀.
,, 3. The same of *C. daviesana* Smith ♀.
,, 4. The same of *C. floralis* Eversm. ♀.
,, 5. The same of *C. succincta* (L.) ♂.
,, 6. The same of *C. fodiens* (Geoffr. *in* Fourcr.) ♂.
,, 7. The same of *C. daviesana* Smith ♂.
,, 8. The same of *C. floralis* Eversm. ♂.

with brown pubescence in fresh specimens. Rather large species) ..... *C. succincta* (L.).

— Apex of abdominal tergite 1 black or pitchy. Malar space 7-8 times as broad as long (as in fig. 2). Pale abdominal pubescent bands white. First tergite with long hairs at sides and at extreme base only ..... 5.

5. Smaller species (L. 7-9 mm.). Pale apical band of first tergite continuous in good specimens. Thoracic pubescence greyish rather than brown, even in fresh specimens ..... *C. marginata* Sm.

— Larger species (L. 8-10·5 mm.). Pale apical band of first tergite interrupted. Thoracic pubescence typically bright reddish-brown (redder than in *fodiens*) . *C. similis* Schenck.

6. Malar space (fig. 4) about three times as broad as long. Second tergite with a pale basal band. Hairs of clypeus sparse, not hiding the surface. First tergite with fewer long hairs ..... *C. floralis* Eversm. (=*montana* Mor.).

— Malar space 6-7 times as broad as long (fig. 3). Second tergite without a pale basal band. Hairs of clypeus dense, semi-procumbent, hiding the surface. First tergite at base with numerous long hairs even on disc of basal part of dorsal surface ..... *C. daviesana* Sm.

Males.

1. Large species (L. about 12-13 mm.). Abdominal surface with long hairs throughout, no pale apical pubescent bands. Malar space a little longer than broad .. *C. cunicularia* (L.).

— Smaller species (L. less than 11 mm.). Abdomen mainly with very short hairs, with distinct apical pubescent pale bands. Malar space at most half as long as broad ..... 2.

2. Sixth sternite with a deep, round, well-defined fovea on each side. Malar space (fig. 5) about half as long as broad. Hind basitarsus (fig. 9) narrow, fully four times as long as broad, second segment not produced dorsally into a strong lobe ..... *C. succincta* (L.).

— Sixth sternite without such foveae ..... 3.

3. Sixth sternite basally at sides produced into small teeth (sometimes more or less hidden by the tergite), disc of sternite flat, sides not depressed. First tergite more shining and less punctured than in any species except *floralis*. Malar space (fig. 7) one-third times or rather more as long as broad. Hind basitarsus (fig. 13) about three times as long as broad, second segment somewhat lobate at apex, about one and a half times as long as greatest width ..... *C. daviesana* Sm.

— Sixth sternite without these teeth or, if with traces of them, then the sternite is feebly longitudinally convex and depressed on each side ..... 4.

4. Hind basitarsus about four times as long as broad, second segment more or less dorso-apically lobate, one and a half times as long. Sixth sternite longitudinally convex and depressed at each side ..... 5.

— Hind basitarsus five times as long as broad, second segment twice as long as greatest width (figs. 12 and 14). Sixth sternite flat, unmodified ..... 6.

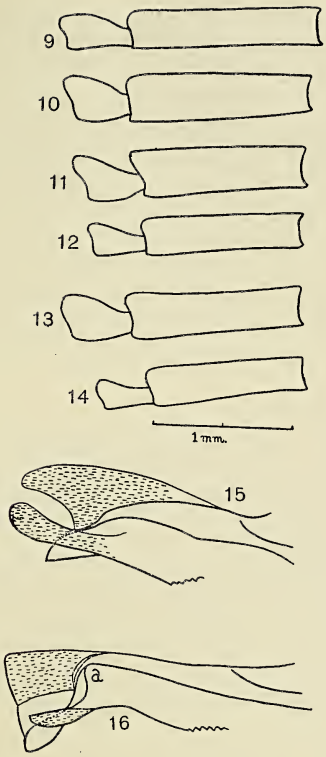

Fig. 9. The first two segments of right hind tarsi of *C. succincta* (L.) ♂.
,, 10. The same of *C. fodiens* (Geoffr. *in* Fourcr.).
,, 11. The same of *C. similis* Schenck.
,, 12. The same of *C. marginata* Smith.
,, 13. The same of *C. daviesana* Smith.
,, 14. The same of *C. floralis* Eversm.
,, 15. Apex of sagittae of male genitalia of *C. similis* Schenck, seen from the right. (More enlarged than other *Colletes* figures.)
,, 16. The same of *C. fodiens* (Geoffr. *in* Fourcr.). a = truncate dorsal keel.

5.* Longitudinally raised disc of sixth sternite without cross-striation, towards base with some large punctures. Sternites 3 and 4 with more complete but less decumbent apical pubescent bands. Second segment of hind tarsi (fig. 11) more lobate. Black dorsal keel of sagitta of genitalia (fig. 15) sinks gradually at apex, in profile not all truncate ..... *C. similis* Schenck. (=*picistigma* Thoms.).

* E. Saunders' (1896 : 175-6) comparison of the sixth sternite of these two species is not, in my opinion, very satisfactory. He identified them correctly, but did not express the differences well.

— Longitudinally raised disc of sixth sternite with microscopic cross-striation but no large punctures at base. Sternites 3 and 4 with apical pubescent bands widely interrupted but pubescence at sides decumbent. Second segment of hind tarsi (fig. 10) less lobate. Black dorsal keel of sagitta sinks suddenly at apex, where it is outwardly reflexed and in profile truncate (fig. 16). *C. fodiens* (Geoffr. *in* Fourcr.)

6. Malar space nearly half as long as broad (fig. 8). Sternites with very feeble apical fringes
..... *C. floralis* Eversm. (=*montana* Mor.).

— Malar space about four times as broad as long (about as in fig. 6). Sternites with dense pale apical pubescent fringes
..... *C. marginata* Sm.

(*b*) Size of *Colletes*.

The size of the host may be expected to have a direct relation with the size of its parasite. Parasitic bees, as far as is known, destroy the egg or first stage larva of the host, so that the relation is with the size of the pollen-store, not directly with that of the host's body.

Table I summarizes the length measurements of some of the female *Colletes* examined (*i.e.* not all specimens studied were measured).

The differences in mean lengths between all pairs of species are significant (see on p. 107), except the difference between *marginata* and *daviesana*, where perhaps too few specimens of the former species have been available, and those between *floralis* and the two species on either side of it. *C. cunicularia* ranges between 12 and 14 mm., with the mean at 13 mm.

(*c*) The flight-period of *Colletes*,

In studying the relation between *Epeolus* and *Colletes*, the flight-period of the host is of the utmost importance. The period of *C. marginata*, for instance, overlaps very little with *C. succincta*, and the same is true of their parasites. Accurate knowledge of this sort is of great assistance in determining the likely host of particular specimens of *Epeolus*. Undoubtedly the ideal method is to carry out extensive observations in one year and one place on all the species together. As this has not been possible, the problem has been approached in a different way. A table has been prepared (Table II) in which all the data on flight-period are gathered together. The summer has been divided into five-day periods and the number of individuals of each sex captured in each period are recorded. The table is based on the combined figures from all the collections I have examined and also from some MS. notes received from corres-

pondents. Unfortunately, a rather high proportion of specimens is not accurately dated, so that the figures are lower than might be expected.

In such a table, where late and early years and northern and southern localities are all combined, the apparent flight-period is longer than that actually experienced in one place and year. But the table gives, nevertheless, an extremely useful basis for comparison with the similar figures for *Epeolus*.

One fact emerges at once from the table. It is highly probable that *C. marginata* and *C. similis* have at least partial second broods. The bimodality in the flight-period is more strongly marked in the males than in the females, probably because the former are shorter lived. Captures made by the Rev. A. Thornley on the Lelant sandhills, W. Cornwall, support this suggestion in *C. marginata*.

In 1937, he captured 1 ♀, 1st July, and 1 ♂, 17th Aug.; in 1930, 1 ♂, 2 ♀♀, 9th July, 1 ♀, 18th July, 2 ♀♀, 31st July, and 5 ♂♂, 12th Aug.

In *C. similis*, there is not such direct observational evidence, but the records are very suspicious. It should be noted that the 6 ♂♂, 1 ♀, recorded for the end of May were obtained by Dr. R. C. L. Perkins near Newton Abbot, S. Devon; the climate here is mild, but the spring must have been a very early one.

The flight of the parasites is probably correlated with that of the female *Colletes* rather than with that of the male, and the maximum might be expected a week or fortnight later.

(*d*) Distribution and habits of *Colletes*.

The chief complication of the study of *Epeolus*-races is the occurrence of so many of the host-species together. There are, however, certain differences in distribution which are of considerable help in assigning the parasites to their hosts.

C. cunicularia (L.) is not attacked by an *Epeolus*, though on the Continent it is the host of *Sphecodes albilabris* (Fab.) (=*fuscipennis* Germar). In England, *C. cunicularia* is confined to the vice-counties of Cheshire, S. Lancs (Saunders, 1896: 179) and Mid-Lancs (Saunders, *l.c.*), where it occurs on the coastal sand-dunes in April and May.

C. floralis Eversm. (=*montana* Mor.) is attacked in N. Germany by *E. montanus* Bischoff. In this country, *C. floralis* is known from Ayrshire, Tiree (Inner Hebrides), Barra (Outer Hebrides; A. R. Waterston), and Ireland, S. Kerry, E. Cork, Clare, Wexford and W. Donegal (Stelfox, 1927).

In the Ayrshire locality (Irvine Moor), Daglish recorded an *Epeolus*, which Edward Saunders identified as *Epeolus productus* Thoms. (Daglish, 1901). The Daglish collection was

auctioned in 1923 or 1924 and some of the bees were bought by Mr. A. Fergusson, who has been kind enough to lend me the single male *Epeolus* now remaining. The specimen was at first difficult to interpret (see p. 102), but has now proved to be *E. cruciger* (Pz.). The locality is a long way from the next northermost record of either species of *Epeolus* (viz. S. Yorks).

C. marginata Smith is almost entirely a southern and coastal species. It is found inland on the Breck sand area, but otherwise only on the coast. Mr. G. M. Spooner informs me that in Dorset it is strictly coastal, not spreading at all on to the sandy commons which abut on the coastal sand-dunes. In association with this habitat, Mr. A. H. Hamm tells me that at St. Helens, Isle of Wight, the nests are in loose sand and that the entrance of the burrow always falls in when the female leaves the nest. The other species all nest in firmer sand. Careful collecting would almost certainly produce a series of *marginata*-parasites, since its habitat is relatively sharply defined. One such series has been supplied to me by Mr. G. M. Spooner, but otherwise my recognition of *marginata*-parasites has had to be a matter of inference. Locality labels are never sufficiently precise, especially as a few hundred yards may be all that separates an area in which *C. marginata* swarms from one in which other species entirely replace it.

C. marginata is known from the following vice-counties: Cheshire, W. Suffolk, W. Gloster (Perkins, 1924: 138), N. Essex, E. Kent, W. Sussex (Saunders, 1896: 178), Isle of Wight, Dorset, S. Somerset (Perkins, 1924: 138), W. Cornwall, Glamorgan.

Records for Cumberland and S.W. Yorks (F. Smith) are almost certainly due to misidentifications. The records for Surrey and S Devon given by Saunders (1896: 178) require confirmation.

C. marginata is attacked by *E. cruciger* (Pz.) var. *marginatus* Bischoff and almost certainly also by a small race of *E. variegatus* (L.).

C. succincta (L.) is normally restricted to heath-land, the female obtaining her pollen entirely or almost entirely from *Erica* and *Calluna*. Until recently, I had supposed that *C. succincta* was absolutely confined to heath-land areas, but in Sept., 1935, Mr. G. M. Spooner found large colonies at Scolt Head and Blakeney Point, E. Norfolk, on maritime sand. The nests were in firm sand, sometimes when fixed by grass, etc. Both sexes were visiting *Aster tripolium* in large numbers, while a few were also found on *Limonium* sp. and on *Senecio Jacobaea*; no *Erica* or *Calluna* were present. In a number of heath-land areas *C. succincta* is the only species of the genus to be found. But, frequently, in sand-pits, etc., on the edge of heaths, *C.*

fodiens, C. similis and *C. daviesana* also occur (as at Woking and Chobham, Surrey). Nevertheless, it is not difficult to obtain a series which consists with considerable certainty entirely of *Epeolus cruciger* var. *similis* Höppn., the special parasite of *C. succincta*.

C. succincta is known from the following vice-counties: Cumberland, Durham (Harrison, 1931), S.E. and N.E. Yorks (Butterfield and Fordham, 1932), S. Lancs (Gardner, 1901), Cheshire (Britten, *in litt.*), Stafford, Notts (Carr, 1916), N. Lincs (George, 1888), E. Norfolk, W. Norfolk, E. Suffolk, W. Suffolk, Beds, W. Gloster (Perkins, 1924), N. Essex, Herts (Palmer, 1924), Bucks, Surrey, E. Sussex, Berks, S. Hants, I. of Wight, N. Hants, Dorset, N. Somerset, S. Somerset, N. Devon, Lundy, S. Devon, W. Cornwall (Spooner, *in litt.*), Scilly, Merioneth, Glamorgan (Hallett, *in litt.*), Dumfries (Service, 1879), Kintyre (Arran), E. Sutherland, Aberdeen (Grimshaw, *in litt.*), Elgin and in Ireland, S. Kerry, N. Kerry, W. Cork, N. Tipperary, S. Galway, Wicklow, Dublin and W. Mayo (Stelfox, 1927).

C. daviesana Smith is very widespread, usually occurring mixed with the other species. It is apparently commoner in the east and north-east than in the south-west. It is recorded from the following vice-counties: S. Northumberland (Ruspini, 1861), Cumberland, S.E., S.W. and Mid.W. Yorks (Butterfield and Fordham, 1932), S. Lancs and Cheshire (Gardner, 1901), Shropshire (Saunders, 1896), Notts (Carr, 1916), Leicester, E. Norfolk, E. Suffolk, Cambridge (Spooner, 1930), Hunts (Spooner, *in litt.*), Northants (Spooner, *in litt.*), Warwick, Monmouth, W. Gloster (Perkins, 1924), Oxford, N. Essex, W. Kent (Perkins, 1920), E. Kent, Surrey, E. Sussex, Berks, S. Hants, I. of Wight, N. Wilts (Perkins, 1920), Dorset, N. and S. Somerset (Perkins, 1924, S. Devon, Merioneth (Mortimer, 1905), Glamorgan (Hallett, 1914), Edinburgh (Evans, 1900), and in Ireland, Down and Wexford (Stelfox, 1933).

All older authors regarded *C. daviesana* as the only host of *Epeolus*. Bischoff (1930) still regards it as the only host of *E. variegatus* (L.). Perkins (1920), however, and other English entomologists have shown conclusively that *E. variegatus* attacks *C. fodiens* and *C. similis*. Perkins (l.c.) goes so far as to doubt whether *C. daviesana* is ever a host at all. In my opinion, the records of *C. daviesana* as host are too numerous and in some cases (*e.g.* Carr, 1916; Nielsen, 1903) too detailed for all of them to be erroneous. I think (see p. 103) that there is a form of *E. variegatus* attached to *C. daviesana* found in the east but not the west of England. Possibly this eastern form is the only one found on the Continent, but that is pure speculation.

C. fodiens (Geoffr. *in* Fourcr.) is another widespread species, usually found in sandy places. It is recorded from the following vice-counties: Cumberland (Routledge, 1933), S. Lancs (Gardner, 1901), Cheshire, Shropshire (Saunders, 1896: 177), Notts (Carr, 1935), 'Norfolk' (Bridgman, 1879), E. Suffolk, W. Suffolk, Beds (Spooner, *in litt.*), Oxford, Herts (Palmer, 1925), N. Essex (Spooner, *in litt.*), E. Kent, Surrey, W. Sussex (Saunders, 1896), Berks, S. Hants (Saunders, 1896), I. of Wight, Dorset, N. and S Somerset (Perkins, 1924), N. and S. Devon, W. Cornwall, Carnarvon, Merioneth, Glamorgan, Pembroke, Dumfries (Service, 1879).

C. fodiens is probably one host of what may be regarded as the typical form of *E. cruciger* (see p. 105) and it is also the host of one common form of *E. variegatus*.

C. similis Schenk is often found with *C. fodiens* but is more local, being decidedly more attached to the sea-coast and also more western. It is known from the following vice-counties: S.E. Yorks (Butterfield and Fordham, 1932), ? E. Norfolk (specimens in coll. Bridgman were all *C. fodiens*), E. and W. Suffolk, Cambs, Northants (Spooner, *in litt.*), 'Essex' (Nicholson, 1928), E. Kent, Surrey, E. Sussex (Saunders, 1896), Berks, S. Hants, I. of Wight, Dorset, S. Devon, E. Cornwall (Spooner, *in litt.*), W. Cornwall, Scilly Is., Glamorgan (Hallett, 1914), and in Ireland, ? Wexford, Wicklow, Dublin, Louth (Stelfox, 1927).

C. similis is very closely allied to *C. fodiens* and is probably attacked by the same parasite races. It is at any rate attacked by what is practically the same form of *E. variegatus*.

Bischoff (1930) has described an *Epeolus laevifrons* which, it is suggested, is a parasite of *C. similis*. As far as I can gather, the chief evidence for this host-attribution is that parasites had already beeen assigned to *C. daviesana, C. marginata, C. succincta* and *C. fodiens* so that *C. similis* seemed to need one too. *E. laevifrons* was founded on a single specimen allied to *E. cruciger,* but with larger smooth spaces between the punctures of the head. I have looked out for such specimens among the British material I have examined. There is some variation in the size of the shining interstices, but nothing approaching a specific variation. I think we can take it , therefore, that *E. laevifrons* does not occur in England.

II. The parasites.

(*a*) Nomenclature.

The type of *Apis variegatus* Linnaeus, 1758, is preserved in the Linnean collection at Burlington House. It is a male, not now in very good condition. Alfken (1913: 34-36), on the basis of information received from F. D. Morice, corrected his

own and C. G. Thomson's earlier view of *A. variegatus* L. Alfken proposed the name *glacialis* for *E. variegatus* Thomson *nec* L., but left the identification of Linnaeus' species undecided. I have made a careful examination of the specimen (I am much indebted to Mr. A. Savage for help in examining the Linnean collection). The males of this genus are less easy to separate than the females, but I think this specimen is clearly the same as *E. productus* Thomson, 1870. It has the tridentate labrum with discal tubercles nearer the ventral edge than the centre, the sparsely punctured metapleuron, the relatively sparsely punctured anterior surface of the hind femur and of the second abdominal sternite.

Stöckhert (1933 : 65) returns to Alfken's original view, synonymising *glacialis* with *variegatus* L. As shown above, this view is incorrect. *E. glacialis* Alfken is a parasite of *Colletes impunctata* Nylander in N. Germany. In the Alps, this host is present in a varietal form (=*C. alpina* Mor.). Bischoff (1930) has described the *Epeolus* which associates with this host of *E. alpinus,* but Stöckhert, probably correctly, regards *E. alpinus* as no more than a variety or even complete synonym of *glacialis*.

All modern authors identify *Nomada cruciger* Panzer, 1799, with *E. rufipes* Thomson, 1870. Panzer's type should be examined (if still extant), but meanwhile the identification may be accepted. It is convenient to follow Bischoff in regarding the typical form of *E. cruciger* as the race of it which associates with *C. fodiens*. Which form of *E. cruciger* Panzer's type actually belongs to is, of course, quite unknown.

This synonymy may be summarised as follows :—

1. *E. variegatus* (Linnaeus, 1758).
   variegatus F. Smith *in part.*
   productus Thomson, 1870.
   notatus authors (*nec* Christ, 1791).
2. *E. cruciger* (Panzer, 1799).
   variegatus F. Smith *in part.*
   rufipes Thomson, 1870.
3. *E. glacialis* Alfken, 1913.
   variegatus Thomson, 1870, Stöckhert, 1933, *nec* Linnaeus.
   ?alpinus Bischoff, 1930.

(*b*) Separation of the British species of *Epeolus*.

Under the present heading only the more discontinuous distinctions are listed. As will be seen in later paragraphs, many of the variable characters of the species have different means when treated biometrically.

Females.

E. variegatus (L.).	*E. cruciger* (Pz.).
Labrum with apex tridentate (*i.e.* a small emargination, defined by minute teeth, bears another minute tooth in centre).	Labrum bidentate at apex.
(Central tooth rarely indistinct; labrum often hidden by mandibles or by dirt.)	
Two small tubercles on disc of labrum situated on a level a little below the mid-point.	Tubercles far below the mid-point of the labrum.
Top of metapleuron (*N.B.*—not of sides of the propodeum) smooth and shining with few, large, widely separated punctures.	Top of metapleuron much duller, the punctures smaller, more numerous and closer. (Character not quite discontinuous).
Dorsal triangular area of propodeum always shining, only top third sometimes very slightly dull.	Dorsal area of propodeum often considerably alutaceous and dull.
Curved transverse keel across middle of first sternite overhangs the part of the sternite just posterior to it.	Keel joined to part of sternite just posterior to it in a smooth curve.
Second sternite more coarsely and sparsely punctured, more shining.	Second sternite more finely and closely punctured, duller.
Raised margin of pygidial area weaker.	Raised margin of pygidial area stronger and extending further towards anterior margin of segment.
Fifth sternite considerably produced apically and impressed over apical half (absolutely diagnostic character).	Fifth sternite widely rounded at apex, not impressed.
Femora (especially hind pair) largely black-marked, anterior side more coarsely and sparsely punctured (almost entirely red only in six specimens).	Hind femora entirely red. Anterior side duller, more finely and closely punctured.

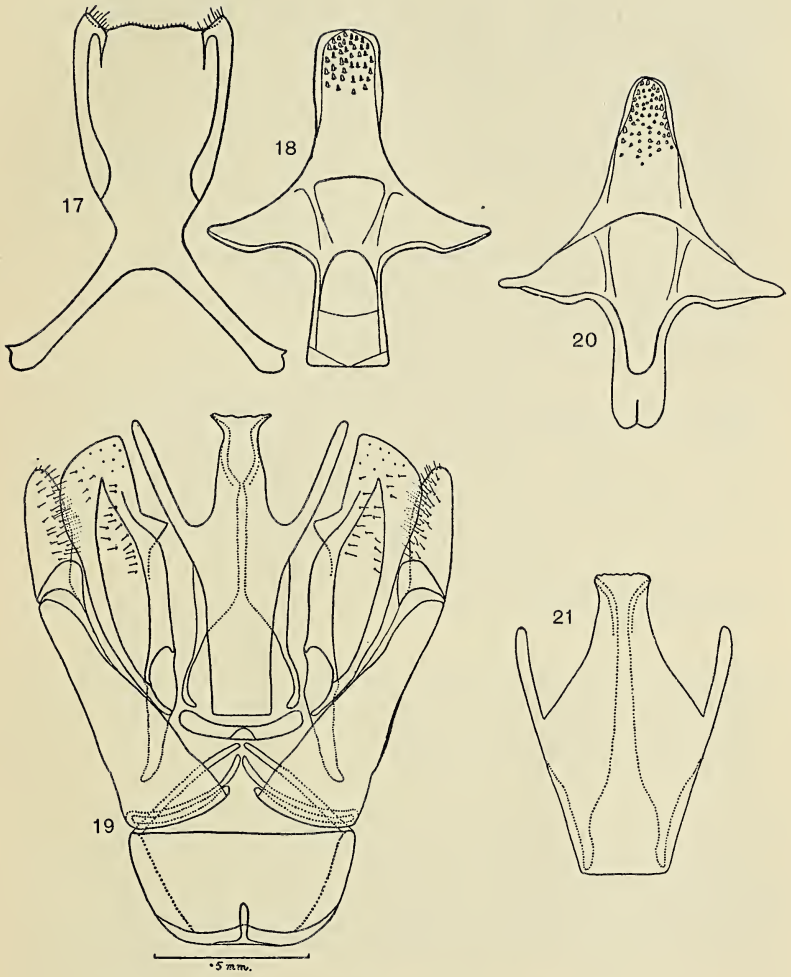

Fig. 17. Eighth sternite of *Epeolus variegatus* (L.) ♂.
,, 18. Ninth sternite of *E. variegatus* (L.) ♂.
,, 19. Dorsal view of male genitalia of *E. variegatus* (L.).
,, 20. Ninth sternite of *E. cruciger* (Pz.) ♂.
,, 21. Sagittae of male genitalia of *E. cruciger* (Pz.).

Males.

E. variegatus (L.).	*E. cruciger* (Pz.).
Labrum as in female, but surface more uneven, so that discal tubercles are less easy to make out (sometimes scarcely distinguishable).	Labrum as in female.
Metapleuron as in female, but puncturation more variable.	Metapleuron as in female, but intermediates running close to *variegatus* not rare.
Transverse keel of first sternite normally as in female but a few intermediates or (very rarely) specimens resembling *cruciger* occur.	Transverse keel as in female.
Femora almost entirely black (only apex very narrowly red).	At least hind femora nearly always with some red at base postero-ventrally. (Only 8 out of 91 males have hind femora black with apex very narrowly red.)
Apical part of hidden ninth sternite parallel-sided (Fig. 18).	Apical part of ninth sternite with the sides convergent (Fig. 20).
Genitalia with lateral process of sagittae as long as the central part. Other differences in genitalia rather indefinite (Fig. 19).	Lateral process of sagittae shorter than central part (Fig. 21).

(*c*) Distribution of the aggregate species of *Epeolus*.

I have seen specimens or know of records of *E. variegatus* (L.) from the following vice-counties: S.E. Yorks, S.W. Yorks (Butterfield and Fordham, 1932), S. Lancs, Cheshire, Notts, E. Norfolk, E. and W. Suffolk, Beds (Chambers, 1933), Worcester, Oxon., N. Essex, E. Kent, Surrey, E. and W. Sussex, Berks, S. and N. Hants, I. of Wight, Dorset, S. and N. Devon, E. and W. Cornwall, Glamorgan.

Quite outside the range of the species, as outlined above, is one male of the series captured by Daglish (Daglish, 1901) on Irvine Moor, Ayrshire, with *Colletes floralis* Eversm. These specimens were identified as *E. variegatus* (*' productus '*) by the late Edward Saunders. Only one male has been available for study, but its structure (including labrum, metapleuron, keel

of first sternite, ninth sternite and male genitalia) agree with *E. cruciger*.

The following is a condensed description of the specimen: labrum black, antennae broken off, anterior pubescent spots of first tergite joined, anterior and posterior spots of first tergite widely joined, lateral and discal spots of third tergite separated by $\frac{1}{3}$, discal spots of third tergite separated by $\frac{1}{2}$, lateral and discal spots of fourth tergite separated by $\frac{1}{2}$, discal spots of fourth tergite separated by $\frac{1}{4}$, discal spots of fifth tergite joined, pygidium dark red to pitchy, hind and mid tibiae with slight, fore tibiae with large dark mark, all femora brown-black with narrow red apex, top of propodeum (especially on disc) rather strongly alutaceous, ten hamuli. Length 7 mm.

Irvine Moor, 8th July, '99 (Daglish).

The date of capture of the specimen supports the association with *C. floralis*, as the date is very early, considering the latitude. Further material would be necessary to establish whether a special race has been developed.

I have seen specimens or know of records of *E. cruciger* (Pz.) also from the following vice-counties: Ayrshire, S.E. Yorks, Notts, Cheshire, N. Lincs (George, 1906), E. Norfolk (Saunders, 1896: 306), W. Suffolk, N. Essex (Saunders, 1896: 306), Bucks, E. Kent, Surrey, Berks, S. and N. Hants, I. of Wight, Dorset, N. and S. Somerset (Perkins, 1924: 145), S. Devon, W. Cornwall, Merioneth, Glamorgan.

(*d*) Evidence for host-attributions.

(1) *C. daviesana* Smith.

There seems little doubt that this bee is the main host of *E. variegatus* in Nottinghamshire (Carr, 1916). The other species of *Colletes* are relatively rare there, and the *Epeolus* were found flying near large colonies of *C. daviesana*. Blair (1920) at Shanklin, I. of Wight, dug out some *Epeolus* pseudo-pupae from amongst the cells of *C. daviesana*. One of these produced a male which has been studied. It is, perhaps, unnecessary to assume (as is suggested in a footnote to Blair's paper) that another species of *Colletes* might have been nesting with *C. daviesana* and acting as the real host.* Nielsen also (1903) gives a substantial account of rearing the same parasite from *C. daviesana*.

Of the Nottinghamshire material, I have examined 24 ♀♀ and 4 ♂♂ (received from Prof. J. W. Carr and Mr. H. P. Jones), also 1 ♂, I. of Wight (Dr. K. G. Blair). Finally, 3 ♀♀,

* Since the above was written, I have seen a ♀ *E. variegatus* dug out of a bank at Kingsley, S. Hants, 10 June, '36, with ♂ ♀ *C. daviesana* by Mr. D. O. Boyd. The bees were in the pupal stage when excavated and emerged 3—7 July, '36.

Wroxham, E. Norfolk, 5th Sept., '02 (G. A. K. Marshall) must, I think, certainly be parasites of *C. daviesana*. The host was caught at the same time and the other possible hosts are all over by that date. These are the only specimens that I can regard as *definitely daviesana*-parasites, though many other specimens from the east of England may be so.

There is no suggestion that *E. cruciger* ever attacks this host.

(2) *C. marginata* Smith.

Perkins (1920) has indicated that this bee is the host of a small form (=*E. marginatus* Bisch.) of *E. cruciger*. The host species has a restricted distribution in this country, so that locality alone is an important guide to the host of any particular specimen of the parasite. From localities where *C. marginata* occurs, a small, early-captured form of *E. cruciger* is found in many collections; in several cases specimens of the host captured on the same day were found in the same collection. Mr. G. M. Spooner lent valuable material definitely associated with the Studland colonies of *C. marginata*. In all doubtful cases, specimens captured later than the end of July were not accepted as parasites of *C. marginata*. The following specimens are regarded as *C. marginata*-parasites: Deal, 4 ♀♀, Aug., '07 (Donisthorpe; Hope Dept.); 2 ♀♀, 15th July, '98 (Chitty; Hope Dept.); 1 ♂, 1 ♀, July, '82 (E. Saunders; B.M.); Wallasey, 1 ♀, 2 ♂♂, 9th July, '10 (Arnold; Hope Dept.); Porthcawl, 2 ♀♀, July, '14, 1 ♂, 1st July, '15, 2 ♂♂, 29th June, '15 (Hallett); Gower Peninsula, 1 ♂, 4 ♀♀ (Hallett); Kenfig, 1 ♂, 3 ♀♀, July, '31 (Hallett); Porteynon, 1 ♂, June, '14 (Hallett); Studland, 3 ♂♂, 6 ♀♀, 19th July, '33, 2 ♀♀, Aug., '31, 1 ♀, Aug., '27, 3 ♂♂, 3 ♀♀, 8th July, '34, 1 ♀, 20th July, '33, 3 ♀♀, 17th July, '30 (Spooner); Mildenhall, 2 ♀♀, July, '95 (Perkins; Cambridge Mus.).

The host of some of the Glamorgan specimens is perhaps a little doubtful as *C. similis* is also present and is an early species.

C. marginata has not previously been suggested as a host of *E. variegatus*, but I think it must be one, as small specimens seem to turn up early in the summer in most *C. marginata* localities. There are 10 ♀♀, 5 ♂♂, captured by Mr. A. H. Hamm (some now in the Hope Dept.) at 'The Dover,' St. Helens, I of Wight, which I think must be associated with this host. *C. marginata* was the only *Colletes* caught (or at any rate caught and preserved) on that occasion (13th-18th July, '99) and the specimens are well below the average in size. I have further seen the following specimens: Studland, 1 ♂, 17th July (Spooner); 1 ♂, St. Helens, July, '95 (E. Saunders; B.M.). A number of Glamorganshire specimens sent by Mr. Hallett

may belong here, but I have excluded them because *C. similis* may have been the host.

(3) *C. fodiens* (Geoffr. *in* Fourcr.).

This is well authenticated as a host of *E. variegatus* (see Perkins, 1920). Unfortunately, in many localities, *C. similis* is also present. The following specimens, however, may be definitely associated with *C. fodiens*: Tubney, Berks, 17 ♀♀, 3 ♂♂, 16th July to 8th Sept. (A. H. Hamm and O.W.R.) (*C. fodiens* is abundant here, *C. similis* does not occur and *C. daviesana* and *C. succincta* are rare); Braunton Burrows, N. Devon, 2 ♀♀, 3rd Aug., '33, 12 ♀♀, 4 ♂♂, 4th Aug., '35 (Spooner; definitely associated with the host); 1 ♀, 'Kirkl.,' 13th Aug., '91 (F. D. Morice; Hope Dept.) (I have not been able to decipher this abbreviation, but there are a number of specimens of *C. fodiens* in the collection with the same data).

As regards the possibility (strongly maintained in Germany) that *E. cruciger* may also attack this bee, see the discussion on p. 113.

(4) *C. similis* Schenck.

This species has also definitely been recorded as a host of *E. variegatus* (Perkins, 1920). The following specimens are, I think, definitely parasites of this species and not of *fodiens*: Whitecliff Bay, I. of Wight, 2 ♀♀, 9th July, '99 (A. H. Hamm) (*C. similis* and no other *Colletes* taken at same place and on same date); 7 ♀♀, Chudleigh, S. Devon (Perkins; Hope Dept.) (two of them labelled as attacking *C. similis*); 1 ♀, Bovey Tracey, S. Devon, 29th July, '15 (Perkins; Hope Dept.) (host noted on the label); 2 ♀♀, 3 ♂♂, Milford, S. Hants, 1st-4th July, '27, and 12th Aug., '31 (H. P. Jones) (host noted on the label); 2 ♀♀, Milford, July, '09 (Morice; Hope Dept.); 9 ♀♀, 10 ♂♂, Beaulieu, S. Hants (Le Marchant; B.M.) (in the Le Marchant collection there is a long series of *C. similis* (and no other *Colletes*) collected on the same dates as these parasites); 5 ♀♀, St. Minver, E. Cornwall (Le Marchant; B.M.) (in the Le Marchant collection is a long series of *C. similis* (and no other *Colletes*) collected on the same dates as these parasites).

As regards the possibility that *E. cruciger* may also attack this bee, see the discussion on p. 113.

(5) *C. succincta* (L.).

This is the best authenticated host of *E. cruciger,* the two species being frequently (though not always, *e.g.* Glamorgan (Hallett)) found together on heaths at the end of the summer.

Höppner (1899) described this form of *E. cruciger* as a new species, *E. similis*. I have regarded all specimens of *E. cruciger* captured later than 24th Aug. as certain parasites of *C. succincta*. Earlier captured specimens are also accepted when there is confirmatory evidence, as it has been shown (Table II) that females of *C. succincta* are often common from the end of July onwards. The following specimens are regarded as *C. succincta* parasites: 1 ♀, Oxshott, 11th Sept., '27 (O.W.R.); 1 ♂, 2 ♀♀, Bagshot, 20th Aug., '34 (O.W.R.); 1 ♀, Horsell, 10th Sept., '15, 3 ♀♀, Woking, 28th Aug., '90, 30th Aug., '90, and 5th Sept., '96 (Morice; Hope Dept.); 3 ♀♀, Chobham, 29th Aug., '90, and 10th Sept., '91 (Morice; Hope Dept.); 1 ♀, Horsell, 28th Aug., '14 (Champion; Hope Dept.); 1 ♀, Woking, 8th Sept., '91, 1 ♀, Chobham, 10th Sept., '91 (Thornley; Nottingham Mus.); 2 ♀♀, Studland, 29th Aug., '06, and 31st Aug., '06 (Yerbury; Hope Dept.); 2 ♀♀, Studland, 1st Sept., '14, 2 ♀♀, Winfrith, 6th Sept., '17, and 25th Aug., '08, 1 ♂, 4 ♀♀, Arne, 3rd Sept., '15, 1 ♀, nr. Poole, 24th Aug., '15, Dorset (Haines); 1 ♀, Studland, 31st Aug., '33, 1 ♀, Tadnoll Knoll, 7th Sept., '27, 2 ♀♀, Warmwell Heath, 24th Aug., '27, and 29th Aug., '27, Dorset (Spooner); 9 ♀♀, Totland Bay, I. of Wight, 28th-31st Aug., '05 (Le Marchant; B.M.); 3 ♀♀, Dartmoor, S. Brent, Aug., '19 (Perkins; Hope Dept.); 12 ♂♂, 8 ♀♀, Bovey Tracey, S. Devon, 27th Aug., '15 (Perkins; Hope Dept.); 1 ♀, Lizard, 31st Aug., '28 (Spooner); 2 ♀♀, Kennack, W. Cornwall, 5th Sept., '33 (Thornley); 3 ♀♀, Allerthorpe Common, Yorks, 26th Aug., '18, 12th Sept., '29, 14th Sept., '29 (Fordham; Liverpool Mus.).

There is no suggestion that *E. variegatus* ever attacks *C. succincta*.

(*e*) Relation of parasite to host.

The most substantial account is that of Nielsen (1903); certain details are also recorded by Blair (1920). In Denmark, Nielsen found the larva of *E. variegatus* (L.) (=*E. productus* Thoms.) in at least one-third of the cells of *C. daviesana*. The larva kills either the egg or at least the very young larva of the host and feeds on the pollen-store. The more mature larva of *Epeolus* has a remarkable flattened form and eats the entire food-supply; *Colletes*, on the other hand, always leaves some of the food which is plastered round the cell before pupation. Cells containing *Epeolus* are therefore more transparent. Blair (1920), in April, found *E. variegatus* in the peculiar prepupal stage. The larva is then hard-shelled, with the spiracles large and heavily sclerotized. This stage moults into the pupa early in June.

(*f*) Analysis of the variation in *E. variegatus* (L.) and *E. cruciger* (Pz.).

The method adopted has been to discover by preliminary examination which structures, etc., show variation and to define a number of classes for each character. Thus, body-length is tabulated in half-millimetre classes, while the colour of the scutellum is tabulated in three arbitrary classes (p. 109). The class of twenty-three characters (some only in one sex or species) have been tabulated for each specimen (where possible).

When these characters have been tabulated, it is possible to treat the problem biometrically, to see which of the varying characters shows a type of distribution differing from the 'normal' (in the statistical sense) or to test whether a particular group of specimens differs from the mean of the species and to calculate correlations.

If only two or three hosts were involved, the problem would be relatively simple. But unfortunately there are five possible hosts, and the material available was too small to exhibit five separate 'peaks' clearly (supposing such existed), unless the five forms were very distinct, in which case they would have been detected by ordinary taxonomic methods.

It is therefore necessary to combine taxonomic with biometrical methods, that is to say, the material has to be sorted out in a preliminary way before biometrical methods are applied. There is a danger here of a vicious circle, for evidently if *merely similar-looking* specimens were picked out, biometric study would naturally tend to show that each selected group was distinct. Actually habitat and date have been principally used to define the preliminary groups, size to a small extent, colour not at all. The evidence has already been given in full in each case (paragraph (*d*)), and I believe that nearly all the specimens which I have treated as parasitic on a particular host really were so. The number of specimens actually labelled by the collector as associating with a particular host was too small to be very helpful.

In the following tabulation of variation (fuller data given in Tables IV—XXIX), the proportions of the various classes are given for each host-race separately whenever there is any indication that the variation is of racial significance. There are simple statistical methods (see Fisher, 1928, p. 75) for calculating whether the proportions of the classes in any two races differ more than would be expected in two random samples of the same population. The value of P given in some of the tables expresses the chance that the deviations are due to random sampling; *i.e.* P = ·05 (the conventional level of significance) implies that there is only one chance in twenty that the examples could have been drawn from the same population (*i.e.* belong to

one homogeneous race). Unfortunately, this method cannot be applied where the number of specimens in any one class falls below five. Where this happens, the statistical tests have not been applied. Nevertheless, it will be seen in a number of cases that the figures for, *e.g.* the males, though not significant, show differences similar to the females.

Where the characters are strictly numerical (*e.g.* length of body, number of hamuli) the ordinary formula for testing the significance of the difference between two means (Fisher, *l.c.*, p. 107) has been applied.

(*g*) Tabulation of characters (full data in the tables).

(1) Dates of capture.

These are given in full in Tables IIIA and IIIB, each sex and race being recorded separately and the relevant period being divided into five-day intervals. The data must be treated with caution. Date of capture has partly been used to assign *E. variegatus* attacking *C. marginata,* and *E. cruciger* attacking *C. marginata* and *C. succincta,* to their respective hosts. The significance of the differences in the flight-periods of these races should not be tested statistically, though, if my views are correct, they are biologically valid.

(2) Colour of the labrum.

The type of variation is rather different in the two species and to some extent sexually.

E. variegatus. ♀: Entirely black or pitchy, 18 specimens; red with very large (subconfluent) lateral dark spots, 65; red with large separate dark spots, 113; red with small dark spots, 49; entirely red, 26.

♂: Entirely black, 94; black with small apical red spot, 3; black with two small lateral red spots, 6; black with two small lateral red spots and a small apical one, 2.

E. cruciger. There is some indication that the variation is racial, at any rate in the female. The data are presented in Table IV. The following classes are recognised: Entirely black; black with two or three small red spots; red with two large black spots; entirely red or with a small basal black spot. For making a statistical test the first three classes have been grouped together, and it is found that there is a significant tendency for the female *marginata*-parasites to have a redder labrum than parasites of *C. succincta.*

(3) Colour of the antennae.

In *E. variegatus* the scape is black, but the third segment is often partly pale. Two classes may be recognised: apex more or less narrowly reddish beneath; entirely pitchy or black.

It would appear from the data in Table V that female *marginata*-parasites tend to have the segment redder than usual and that female *fodiens*-parasites tend to have it darker than usual, but the numbers are not large enough to apply any test of significance.

In *E. cruciger* both the scape (Table VI) and the third antennal segment (Table VII) vary in colour. In the scape the following classes have been recognised (in the male the scape is always black): red or mainly red beneath; distal half red beneath; narrowly red at apex beneath; black or pitchy. For the purpose of statistical test the first three classes are grouped together, and it is found that the antennal scape is significantly redder in parasites of *C. succincta* than in parasites of *C. marginata*.

The differences in the colour of the third antennal segment are not significant.

(4) Colour of the pronotal tubercles.

The invasion of the red tubercles by black pigment in the female is a gradual process, but two classes can be recognised: those with the tubercles entirely or mainly red, and those with them entirely or mainly black. All males of both species have the tubercles black. From Tables VIII and IX it will be seen that in *E. variegatus* parasites of *C. marginata* and *C. fodiens* tend to have redder tubercles than parasites of *C. daviesana* and *C. similis*. The numbers, however, are too low to test statistically. In *E. cruciger*, the differences between parasites of *C. marginata* and *C. succincta* are not significant.

(5) Colour of the lateral lobes of the scutellum.

These are always black in the males. In the females there are three classes: entirely black or with the tip (posterior angle) very narrowly red; tip considerably red or large disc red; entirely red. The full data will be found in Tables X and XI.

It will be seen that in *E. variegatus*, the parasites of *C. marginata* tend to have redder lateral lobes than usual, but the numbers are too low to test; the differences between the other races are not significant. In *E. cruciger* (if the first two classes are grouped together) the lateral lobes are significantly darker in parasites of *C. succincta* than in those of *C. marginata*.

(6) Colour of the central lobe of the scutellum.

In the males the scutellum is always entirely black. In the females there are three classes: entirely red or with a very narrow black anterior border; red with anterior $\frac{1}{3}$ to $\frac{1}{2}$ black or black with two large, ill-defined red spots; entirely black. The

variation is not correlated with the nature of the host. The classes occurred in the following proportions :—

E. variegatus ♀ : 200; 64; 9.
E. cruciger ♀ : 284; 21; 8.

(7) Separation on disc of tergite of anterior pubescent spots on first tergite of males.

The anterior spots of white pubescence may meet or be separated, but the variation does not appear to be correlated with the nature of the host. Three classes may be recognised: spots joined; narrowly separated; widely separated. These classes occurred in the following proportions :—

E. variegatus ♂ : 61; 23; 16.
E. cruciger ♂ : 87; 3; 0.

(8) Separation of anterior from posterior pubescent spots of first abdominal tergite.

These white pubescent spots may be widely separated or more or less joined at the sides. The following classes may be recognised: widely separated; narrowly separated; narrowly joined; widely joined.

In the males the material is not sufficient to justify analysis according to host, but the classes occur in the following proportions :—

E. variegatus ♂ : 3*; 1; 1; 103.
E. cruciger ♂ : 2 ; 1; 10; 78.

In the females the classes have been reduced to two (separated, joined) for purposes of analysis; the figures will be found in Table XII. In *E. variegatus* it would appear that the spots are more often joined than usual in *marginata* parasites (figures unsuitable for statistical test). The *fodiens* parasites have the spots significantly less often joined than either *daviesana* or *similis* parasites; the two latter do not differ significantly from one another.

In *E. cruciger* the two recognised races do not differ significantly.

(9) Separation of lateral from discal pubescent spots of second tergite.

These spots are always widely joined in both sexes of *E. cruciger* and in the male of *E. variegatus*. In the female of the latter species the same classes can be recognised as in (8).

The results are given in Table XIII, but none of the differences is significant.

* Specimens in bad condition; classification doubtful.

(10) Separation of lateral from discal pubescent spots of third tergite.

When separated, the distance separating the spots can be expressed as a fraction (1, $\frac{2}{3}$, etc.) of the width of the lateral spot (measured transversely). When the spots are joined, two classes are recognised: narrowly joined; widely joined. The results are given in Tables XIV and XV. The figures for the males are too small for analysis. In the females of *E. variegatus* the *marginata* parasites would appear to have the spots closer together than in the other races (figures unsuitable for statistical test). The *similis* parasites have the spots significantly closer together than either the *daviesana* or *fodiens* parasites; the two latter do not differ significantly from one another. In *E. cruciger* females the spots are significantly closer together in the *succincta* than in the *marginata* parasites.

(11) Separation of discal pubescent spots of third abdominal tergite in the male, expressed as a fraction of the transverse width of the spot.

The number of specimens is not sufficiently large to analyse according to hosts. The following figures were obtained:—

Separation of spots:	1-2	$\frac{1}{2}$-$\frac{2}{3}$	$\frac{1}{4}$-$\frac{1}{3}$
E. variegatus ♂ ...	10	69	30
E. cruciger ♂ ...	21	58	12

(12) Separation of lateral from discal spot of fourth abdominal tergite, expressed as a fraction of the transverse width of the lateral spot.

This character was not tabulated for *E. variegatus* females.

The following classes were recognised: 1 or more; $\frac{2}{3}$-$\frac{1}{2}$; $\frac{1}{3}$-$\frac{1}{4}$; narrowly joined; widely joined. In the males the figures are too small to analyse and in the females of *E. cruciger* the racial difference was not significant. The classes occurred in the following proportions:—

	1 or more.	$\frac{2}{3}$-$\frac{1}{2}$.	$\frac{1}{3}$-$\frac{1}{4}$.	Narrowly joined.	Widely joined.
E. variegatus ♂ ...	10	72	20	2	1
E. cruciger ♀ ...	1	46	125	75	64
E. cruciger ♂ ...	2	32	26	24	7

(13) Separation of the discal pubescent spots of fourth tergite, expressed as a fraction of the transverse width of discal spot.

The classes are the same as in the previous character (12). No tabulation was made for *E. variegatus* ♀.

In the males the classes occurred in the following proportions :—

E. variegatus ♂ ...	1	31	74	0	0
E. cruciger ♂ ...	0	22	67	1	1

The figures for *E. cruciger* female will be found in Table XVI. It will be seen that the spots are significantly closer together in the parasites of *C. marginata* than they are in those of *C. succincta*.

(14) Separation of discal pubescent spots of the male fifth tergite, expressed as a fraction of the transverse width of the spot.

The following classes were recognised: 1, $\frac{2}{3}$-$\frac{1}{2}$, $\frac{1}{3}$-$\frac{1}{5}$, joined. The results of tabulation, which are unsuitable for statistical treatment are found in Tables XVII and XVIII.

(15) Colour of male pygidium (seventh tergite).

The following classes were recognised: entirely red or dark red; apical $\frac{1}{2}$-$\frac{1}{4}$ red, base black; entirely black or pitchy. The results will be found in Tables XIX and XX.

(16-18) Colour of tibiae.

In the females of both species the tibiae are always red. In the males, three stages were recognised: red or with a very small central dark mark; moderate or large dark mark; mainly dark. The results will be found in Tables XXI and XXII.

(19-20) Colour of the mid and hind femora.

In *E. variegatus* male the femora are all entirely black. In *E. cruciger* female they are entirely red (1 ♀, Stephens coll., Brit. Mus., no locality, has base of mid and hind femora considerably black marked). In *E. variegatus* female and *E. cruciger* male the following stages have been recognised: black or mainly black; red with a more or less extensive black mark behind or beneath; mainly or entirely black.

The results will be found in Tables XXIII and XXIV. It will be seen that in *E. variegatus* female there is a significant tendency for the mid femora of *fodiens* parasites to be redder than those of *similis* or *daviesana* parasites. The numbers of the *marginata* parasites are too few to treat statistically. There are no significant differences in the hind femora. The differences between the two recognised races of *E. cruciger* male are not significant.

(21) Colour of ventral side of hind coxae in *E. cruciger* female.

The following stages were recognised: distal $\frac{1}{3}$ or less red; distal $\frac{1}{2}$-$\frac{1}{3}$ red; entirely or almost entirely red. There was found to be no racial variation in this character (see Table XXV).

(22) Sculpture of the propodeum in *E. cruciger* female.

According to Bischoff (1930), the form associating with *C. marginata* tends to have a duller, more sculptured propodeum. It is very difficult to classify the stages of this character, but an attempt was made for 55 ♀♀ associating with *C. succincta* and 29 ♀♀ associating with *C. marginata*. The results were as follows:—

	Sculpture.			
Parasites of	Strong.	Moderate.	Weak.	Absent.
C. succincta ...	30	11	13	1
C. marginata ...	12	9	8	0

If anything, therefore, the sculpture is weaker in the British *marginata* parasites.

(23) Number of hooks or 'hamuli' on the hindwings.

This ranges from 9-15 in *E. variegatus* and from 9-13 in *E. cruciger*. The numbers will be found tabulated in Tables XXVI and XXVII. None of the differences in average number is significant except that between females of *E. variegatus* parasitising *C. similis* and *C. fodiens*. A discussion of hamuli-number will be found elsewhere (p. 118).

(24) Length of body in half-millimetres.

A specimen with length '7·5' is a member of the class 7·25—7·75 mm.

All the differences in average size are significant except the following: *E. variegatus*, females, *fodiens* parasites compared with *similis* or *daviesana* parasites; male, *fodiens*, *similis* and *daviesana* parasites do not differ significantly among themselves, nor do the *marginata* parasites differ significantly from the *daviesana* ones (see Tables XXVIII and XXIX). The size differences are also discussed later (p. 118).

(*h*) Does *E. cruciger* parasitize *Colletes fodiens* and *C. similis*?

Bischoff treats the first of the above two species of *Colletes* as the host of the so-called typical form of *E. cruciger*. As far as I know there are no direct observations proving this relationship; there are certainly no direct observations in this

country. There are, however, certain features in the variation of the parasite that strongly suggest that Bischoff's opinion is correct.

It will be seen in the tables of variation of *E. cruciger,* a fourth row of figures ('other specimens') has been obtained by subtracting the class-frequencies of *succincta* and *marginata* parasites from the frequencies in the species as a whole. The fourth row of figures is derived from specimens of the following kind: (*a*) parasites of *C. succincta* which could not be assigned to their host owing to lack of data, (*b*) the hypothetical parasites of *C. fodiens* and *C. similis,* and (*c*) possibly a few (but certainly an insignificant number) of the parasites of *C. marginata.* If specimens of type (*b*) exist, they would account for any marked difference between the figures of the fourth row and the frequencies for definite parasites of *C. succincta* and *C. marginata.*

Such differences exist in the frequencies of the following characters:—

Lateral lobes of scutellum (♀). The *succincta* parasites have these lobes significantly ($P < \cdot 01$) more often dark than do the specimens in row four. The latter do not differ significantly from either the frequencies in the species as a whole or from those in *marginata* parasites. The anterior and posterior pubescent spots of the first abdominal tergite (♀) are significantly ($P < \cdot 01$) less often joined in the *succincta* parasites than they are in the specimens in row four. The latter do not differ significantly from either the frequencies in the species as a whole or from those in *marginata* parasites.

The separation of the lateral and discal spots of the third tergite (♀):—

In *succincta* parasites: not joined in 57 specimens.

In *marginata* parasites: joined in 1 out of 36 specimens.

In other specimens: joined in 20 out of 200 specimens (*i.e.* 1 out of 10).

This difference is perhaps significant.

The separation of the lateral and discal spots of the fourth abdominal tergite (♀):—

	Separated.	Joined.
All specimens	172	139
Succincta parasites ...	41	16
Marginata parasites ...	28	8
Other specimens ...	103	115

When the fourth row is compared with the first P lies between ·02 and ·01, when compared with the other two rows P is less than ·01. The differences in frequencies are therefore significant.

The problem can be treated in another way. If the specimens which have been regarded as parasites of *C. marginata* are set on one side, the remaining material can be analysed separately. It consists of (*a*) the parasites of *C. succincta*, (*b*) the hypothetical parasites of *C. fodiens* and *C. similis*, and (*c*) possibly a few parasites of *C. marginata*. If parasites of *C. fodiens* and *C. similis* exist they would be expected to occur earlier than and to be a little smaller than the parasites of *C. succincta*. As a first step, therefore, the correlation has been calculated between size and date of capture in the specimens left over when the *C. marginata* parasites are set aside. The correlations work out as:—

Female $r = +\cdot2158$ ($P < \cdot01$).
Male $r = +\cdot4102$ ($P < \cdot01$).

There is thus a very significant tendency for the later captured specimens to be larger. The higher value of the correlation obtained in the males is perhaps due to the less complete elimination of real *C. marginata* parasites.

One other character has been treated in the same way, *viz.* the correlation of the degree of separation of the lateral and discal pubescent spots of the fourth tergite with date of capture. The analysis in this case is much less satisfactory, since the measure of separation is only roughly quantitative. The following correlations were obtained:—

Female $r = +\cdot2098$ ($P < \cdot01$).
Male $r = -\cdot6712$ ($P < \cdot01$).

Thus in the females the later a specimen is captured the more widely separated are the spots of the fourth tergite. This agrees with the figures already given (p. 114). The significance of this result is apparently considerably lessened by the reverse correlation observed in the males. Some support, however, for the reality of a reverse correlation in the male is found in the following figures:—

Separation of spots of fourth tergite (♂).

	Separated.	Joined.
All specimens	60	31
Succincta parasites ...	5	9
Marginata parasites ...	14	1
Other specimens ...	41	21

Thus the 'other specimens' have the spots more separated than the *succincta* parasites, a reverse of the position in the female.

The preceding evidence suggests that *C. fodiens* and probably also *C. similis* are parasitised by a race of *E. cruciger*. This preliminary conclusion, however, must be regarded as only tentative until direct observations are forthcoming.

(*i*) Characters of the races.

It is evident that only a very few of the apparent differences between the races are significant. This is in part due to the small number of specimens available for the comparisons. The significant (or probably significant) characters of the races may be summarised as follows:—

E. variegatus.

I. *Marginata* parasites.

Males appear early in July. Female third antennal segment probably redder than in other races. Female pronotal tubercles probably redder than in *daviesana* and *similis* parasites. Female lateral lobes of the scutellum probably redder than in the other races. Female anterior and posterior pubescent spots of first tergite probably more confluent than in other races. Female spots of third tergite probably less widely separated than in *daviesana* and *fodiens* parasites. Both sexes smaller than the other races.

II. *Daviesana* parasites.

Males fly over a long period like their host. Female third antennal segment probably with an intermediate amount of red pigment. Female pronotal tubercles probably darker than in *marginata* or *fodiens* parasites. Female anterior and posterior pubescent spots of first tergite more confluent than in *fodiens* parasites, probably less so than in *marginata* parasites. Female spots of third tergite more widely separated than in *similis* parasites. Female mid femora darker than in *fodiens* parasites.

III. *Similis* parasites.

Both sexes fly mainly in July. Female third antennal segment probably with an intermediate amount of red pigment. Female pronotal tubercles probably darker than in *marginata* and *fodiens* parasites. Female anterior and posterior pubescent spots of first tergite more confluent than in *fodiens* parasites, probably less so than in *marginata* parasites. Female spots of third tergite more confluent than in *daviesana* or *fodiens* parasites. Female mid femora darker and hindwings with more hooks than in *fodiens* parasites.

IV. *Fodiens* parasites.

Both sexes fly in August and the second half of July. Female third antennal segment probably darker than in the other races. Female pronotal tubercles probably redder than in *daviesana* and *similis* parasites. Female anterior and posterior pubescent

spots of the first abdominal tergite less confluent than in the other races. Female spots of the third tergite more widely separated than in *similis* parasites. Females with mid femora redder than in *daviesana* and *similis* parasites. Female hindwings with fewer hooks than in *similis* parasites.

E. cruciger.

I. *Succincta* parasites (=var. *similis* Höppner).

Both sexes fly in August and September. Female labrum blacker, antennal scape redder, lateral lobes of the scutellum blacker, lateral and discal spots of third tergite more confluent, discal spots of fourth abdominal tergite less confluent than in *marginata* parasites. Size larger.

II. *Marginata* parasites (=var. *marginatus* Bischoff).

Both sexes fly in July. Female labrum redder, antennal scape blacker, lateral lobes of scutellum redder, lateral and discal spots of third tergite less confluent, discal spots of fourth tergite more confluent than in *succincta* parasites. Size smaller.

III. *Fodiens* and probably *similis* parasites.

Size and flight period intermediate between *succincta* and *marginata* parasites. Female lateral lobes of the scutellum more often red than in *succincta* parasites. Female anterior and posterior pubescent spots of the first abdominal tergite less confluent than in *succincta* parasites; female spots of third tergite more confluent and of fourth tergite less confluent than in the other two races. Female spots of fourth tergite more confluent than in *succincta* parasites.

In view of the very small interracial differences in *E. variegatus* and *E. cruciger,* it is interesting to compare the two species in the same characters as have been used in separating the races.

Seventeen comparisons are available in the males and thirteen in the females. In the males all the characters differ significantly except separation of the discal spots of the fourth tergite. In the females all the characters differ significantly. The greater apparent differences between the species is certainly due in part to the much larger material used in the comparisons. A difference in the frequency of classes which is not significant when less than 100 specimens are available may become highly significant when 250-300 specimens are compared. But the data also support the view that the races are still very far from being distinct species.

(*j*) Non-racial variation.

Certain characters of the species show correlation with general climatic conditions. The climatic feature examined was the July isotherm; specimens of *Epeolus* were available from areas surrounded by each of the isotherms from 64°-60° F. inclusive. The correlations between size, hamuli number and July temperature have been calculated with the following results :—

	E. variegatus female.		*E. cruciger* female.	
Correlation.	r.	P.	r.	P.
Size × hamuli ...	+·2890	< ·01	+·4065	< ·01
Size × July isotherm	+·148	betw. ·02 and ·01	−·04	not sign.
Hamuli × July isotherm ...	−·0041	not sign.	−·153	betw. ·02 and ·01

Thus it would appear that with a warmer July climate *E. variegatus* female tends to be larger and *E. cruciger* female to have fewer hamuli.

A somewhat similar observation of variation in the honey-bee by Alpatov (1929) showed that southern specimens tend to be smaller and to have more hamuli (*i.e.* the reverse of the conditions in *Epeolus*). In view of the smallness of the correlations and of the insufficiency of material from certain areas in *Epeolus*, the variation in relation to climate need not, perhaps, be regarded as proved.

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Length in mm. of species of *Colletes* (females).

Species.	Total no. of specimens.	Length in mm. 7	7.5	8	8.5	9	9.5	10	10.5	11	11.5	Mean.
marginata	9	1	1	4	2	1	—	—	—	—	—	8.05
daviesana	47	3	9	7	9	13	3	2	1	—	—	8.45
floralis	5	—	—	1	0	4	—	—	—	—	—	8.80
similis	53	—	—	4	15	22	8	3	1	—	—	9.00
fodiens	62	—	—	1	8	19	21	6	5	2	—	9.35
succincta	79	—	—	—	2	13	13	23	19	7	2	10.00

TABLE II.

Time of appearance of species of *Colletes*.

Species.	Sex.	May 27-31	June 1-5	6-10	11-15	16-20	21-25	26-30	July 1-5	6-10	11-15	16-20	21-25	26-30	August 31-4	5-9	10-14	15-19	20-24	25-29	September 30-3	4-8	9-13	14-18	19-23
marginata	♀	—	—	—	—	—	—	—	2	19	3	9	4	3	4	15	0	0	0	2	—	—	—	—	—
	♂	—	—	—	—	1	0	1	14	15	8	6	0	0	0	1	6	1	—	—	—	—	—	—	—
daviesana	♀	—	—	—	—	—	1	0	4	6	15	9	9	9	8	11	3	6	19	0	0	5	—	—	—
	♂	—	—	—	1	3	4	18	5	9	7	7	10	6	14	5	0	1	0	0	0	0	0	1	—
floralis	♀	—	—	—	—	—	—	—	—	2	5	3	1	6	0	4	0	1	1	—	—	—	—	—	—
	♂	—	—	—	—	—	—	—	1	29	2	1	5	5	—	—	—	—	—	—	—	—	—	—	—
similis	♀	1	0	0	0	1	0	2	4	10	2	4	5	8	21	13	31	24	7	2	0	0	0	1	—
	♂	6	0	0	0	1	2	3	3	22	11	2	6	4	9	13	5	4	2	—	—	—	—	—	—
fodiens	♀	—	—	—	—	—	—	1	4	4	6	9	8	10	6	23	7	7	13	0	1	—	—	—	—
	♂	—	—	—	—	3	1	2	7	5	41	7	17	8	6	19	7	1	4	—	—	—	—	—	—
succincta	♀	—	—	—	—	—	—	—	—	—	—	—	7	4	4	7	21	21	20	27	24	15	15	0	2
	♂	—	—	—	—	—	—	1	0	1	1	4	5	6	14	19	23	16	12	13	16	4	—	—	—

In addition to the above records one ♀ of *C. succincta* was captured between 24th and 28th Sept. and one between 29th Sept. and 3rd Oct., while 6 ♂♂ were captured between 24th and 28th Sept. The latter specimens came from Golspie, Sutherland (J. W. Yerbury).

TABLE IIIA.

Time of appearance of *Epeolus variegatus*.

Specimens.	Sex.	June 16-20	21-25	26-30	July 1-5	6-10	11-15	August 16-20	21-25	26-30	31-4	5-9	10-14	15-19	20-24	25-29	September 30-3	4-8
All specimens -	♀	2	0	1	15	8	3	23	12	13	25	26	15	3	7	0	2	4
	♂	—	—	—	8	4	10	7	2	2	6	4	1	—	—	—	—	—
With *marginata*	♀	—	—	—	8	2	—	—	—	—	—	—	—	—	—	—	—	—
	♂	—	—	—	4	1	0	1	—	—	—	—	—	—	—	—	—	—
With *daviesana*	♀	—	—	—	—	—	—	8	3	7	1	0	5	0	0	0	0	3
	♂	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—
With *similis* -	♀	2	0	0	6	2	2	2	2	1	4	1	1	—	—	—	—	—
	♂	—	—	—	3	0	7	2	1	—	—	—	—	—	—	—	—	—
With *fodiens* -	♀	—	—	—	—	—	—	2	1	0	12	9	3	0	4	0	0	1
	♂	—	—	—	—	—	3	0	0	0	4	—	—	—	—	—	—	—

TABLE IIIB.

Time of appearance of *Epeolus cruciger*.

Specimens.	Sex.	June 26-30	July 1-5	6-10	11-15	16-20	21-25	August 26-30	31-4	5-9	10-14	15-19	20-24	25-29	30-3	September 4-8	9-13	14-18
All specimens -	♀	—	—	5	2	11	0	4	8	9	39	45	15	19	15	9	6	1
	♂	2	1	7	0	12	6	3	0	4	17	3	2	12	1	—	—	—
With *succincta*	♀	—	—	—	—	—	—	—	—	—	—	—	4	19	15	9	6	1
	♂	—	—	—	—	—	—	—	—	—	—	—	1	12	1	—	—	—
With *marginata*	♀	—	—	4	2	10	—	—	—	—	—	—	—	—	—	—	—	—
	♂	2	1	5	0	3	—	—	—	—	—	—	—	—	—	—	—	—
Other specimens	♀	—	—	—	—	1	0	4	8	9	39	45	11	—	—	—	—	—
	♂	—	—	1	0	9	5	2	0	4	8	3	1	—	—	—	—	—

Table IV.

Colour of labrum in *Epeolus cruciger*.

Specimens.	Sex.	Class I.	II.	III.	IV.	V.	P.
All specimens -	♂	65	16	5	86	4	
	♀	7	7	51	65	243	
With *succincta* -	♀	1	2	17	20	37	Between ·02 & ·01
With *marginata*	♀	0	1	6	7	29	
Other specimens	♀	6	4	28	38	177	

Note. I = entirely black; II = black with 2-3 small red spots; III = red with two large black spots; IV = I + II + III; V = entirely red or with a small band at base black.

Table V.

Colour of third antennal segment in *Epeolus variegatus*.

Specimens.	Sex.	Reddish at apex beneath.	Segment pitchy or black.
All specimens ...	♂ ...	11 ...	94
	♀ ...	117 ...	152
With *marginata* .	♀ ...	5 ...	4
With *daviesana* .	♀ ...	12 ...	15
With *similis* ...	♀ ...	11 ...	16
With *fodiens* ...	♀ ...	3 ...	29

Table VI.

Colour of antennal scape in *Epeolus cruciger* females.

Specimens.	I.	II.	III.	IV.	V.	P.
All specimens ...	43	56	103	202	110	
With *succincta* ...	10	7	19	36	20	Between ·05 & ·02
With *marginata* ...	1	2	14	17	19	
Other specimens ...	32	47	70	149	71	

Note. I = red or mainly red beneath; II = distal half red beneath; III = narrowly red at apex beneath; IV = I + II + III; V = black or pitchy.

Table VII.

Colour of third antennal segment in *Epeolus cruciger*.

Specimens.	Sex.	I.	II.	III.	IV.	V.
All specimens ...	♀	11	49	102	162	150
	♂	0	0	16	16	74
With *succincta* ...	♀	3	4	14	21	35
	♂	0	0	0	0	14
With *marginata* ..	♀	0	5	9	14	22
	♂	0	0	3	3	12
Other specimens ..	♀	8	40	79	127	93
	♂	0	0	13	13	48

Note. I = red or mainly red beneath; II = distal half red beneath; III = apex narrowly red beneath; IV = I + II + III; V = black or pitchy.

Table VIII.

Colour of pronotal tubercles in *Epeolus variegatus* females.

Specimens.	Entirely or mainly red.	Entirely or mainly black.
All specimens	247 ...	26
With *marginata*	9 ...	1
With *daviesana*	21 ...	6
With *similis*	23 ...	5
With *fodiens*	29 ...	3

Table IX.

Colour of pronotal tubercles in *Epeolus cruciger* females.

Specimens.	Entirely or mainly red.	Entirely or mainly black.
All specimens	251 ...	62
With *succincta* ...	44 ...	13
With *marginata* ...	26 ...	10
Other specimens ...	181 ...	39

Table X.

Colour of lateral lobes of scutellum in *Epeolus variegatus* females.

Specimens.	Black or with small red tip.	Considerably red.	Entirely red.
All specimens	193	68	12
With *marginata*	5	4	1
With *daviesana*	24	3	0
With *similis*	20	6	2
With *fodiens*	23	9	0

Table XI.

Colour of lateral lobes of scutellum in *Epeolus cruciger* females.

Specimens.	Black or with small red tip.	Considerably red.	Entirely red.
All specimens	16	45	252
With *succincta*	6	14	37
With *marginata*	3	4	29
Other specimens	7	27	186

Note.—If the first two classes are combined, the differences in proportion between the parasites of *C. succincta* and *C. marginata* are significant (P is between ·02 and ·01).

Table XII.

Separation of anterior and posterior pubescent spots of the first abdominal tergite in *Epeolus variegatus* and *E. cruciger* females.

Specimen.	Widely separated.	Narrowly separated.	Narrowly joined.	Widely joined.	Separated.	Joined.	P.
E. variegatus.							
All specimens	72	29	56	116	101	172	
With *marginata*	0	0	0	10	0	10	
With *daviesana*	6	1	8	12	7	20*	
With *similis*	4	5	5	14	9	19	Between
With *fodiens*	9	7	7	9	16	16	·05 & ·02
E. cruciger.							
All specimens	190	47	37	38	237	75	
With *succincta*	42	8	3	4	50	7	
With *marginata*	27	4	3	2	31	5	
Other specimens	121	35	31	32	156	63	

Note.—*Less than ·01 compared with *fodiens* parasites.

TABLE XIII.

Separation of lateral from discal spots of second tergite in *Epeolus variegatus* females.

Specimens.	Widely separated.	Narrowly separated.	Narrowly joined.	Widely joined.	Separated.	Joined.
All specimens ...	54	26	46	147	80	193
With *marginata*	4	1	3	2	5	5
With *daviesana*	8	3	8	8	11	16
With *similis* ...	4	3	3	18	7	21
With *fodiens* ...	10	3	2	17	13	19

TABLE XIV.

Separation of lateral from discal spots of third abdominal tergite in *Epeolus variegatus*.

Specimens.	Sex.	Separated. $1\frac{1}{2}$ - 1	Separated. $\frac{2}{3}$ - $\frac{1}{2}$	Separated. $\frac{1}{3}$ - $\frac{1}{4}$	Narrowly joined.	Widely joined.
All specimens	♀	100	169	4	0	0
	♂	6	66	30	5	2
With *marginata*	♀	0	6	4	0	0
	♂	1	4	2	0	0
With *daviesana*	♀	16	10	0	0	0
	♂	0	5	0	0	0
With *similis*	♀	5	21	0	0	0
	♂	0	9	4	1	1
With *fodiens*	♀	16	13	2	0	0
	♂	0	5	1	1	0

NOTE.—In the females, when *daviesana* parasites are compared with *similis* parasites or when the latter are compared with *fodiens* parasites, the value of P is less than ·01.

TABLE XV.

Separation of lateral from discal spots of third abdominal tergite in *Epeolus cruciger*.

Specimens.	Sex.	Separated $1\frac{1}{2}$ - 1	Separated $\frac{2}{3}$ - $\frac{1}{2}$	Separated $\frac{1}{3}$ - $\frac{1}{4}$	Narrowly joined.	Widely joined.	A	B
All specimens	♀	9	179	104	13	8	188	117
	♂	2	34	39	5	11	36	44
With *succincta*	♀	1	36	20	0	0	37	20
	♂	0	5	4	2	3	5	6
With *marginata*	♀	3	27	5	1	0	30	6
	♂	0	10	4	1	0	10	5
Other specimens	♀	5	116	79	12	8	121	91
	♂	2	19	31	3	8	21	33

NOTE.—A = sum of first two columns; B = sum of columns three and four. The value of P when female *marginata* and *succincta* parasites are compared is less than ·01.

Table XVI.

Separation of discal pubescent spots of fourth tergite in females of *Epeolus cruciger*.

Specimens.	Separated 1 or more.	Separated $\frac{2}{3}$ - $\frac{1}{2}$	Separated $\frac{1}{3}$ - $\frac{1}{4}$
All specimens ...	5 ...	217 ...	88
With *succincta* ...	0 ...	50 ...	7
With *marginata* ...	1 ...	22 ...	13
Other specimens ...	4 ...	145 ...	68

Note.—When *succincta* and *marginata* parasites are compared, the value of P is less than ·01.

Table XVII.

Separation of the discal pubescent spots of the fifth tergite in *Epeolus variegatus* males.

Specimens.	Separated 1.	Separated $\frac{2}{3}$ - $\frac{1}{2}$.	Separated $\frac{1}{3}$ - $\frac{1}{5}$.	Joined.
All specimens ...	2	31	67	3
With *marginata* ...	0	5	1	1
With *daviesana* ...	1	3	1	0
With *similis* ...	0	2	10	1
With *fodiens* ...	0	2	5	0

Table XVIII.

Separation of the discal pubescent spots of the fifth tergite in *Epeolus cruciger* males.

Specimens.	Separated $\frac{2}{3}$ - $\frac{1}{2}$.	Separated $\frac{1}{3}$ - $\frac{1}{5}$.	Joined.
All specimens ...	5 ...	63 ...	18
With *succincta* ...	3 ...	7 ...	2
With *marginata* ...	1 ...	10 ...	1
Other specimens ...	1 ...	46 ...	15

Table XIX.

Colour of male pygidium (seventh tergite) in *Epeolus variegatus*.

Specimens.	Red.	Part red.	Black.
All specimens ...	27	4	76
With *marginata* ...	2	1	4
With *daviesana* ...	4	0	1
With *similis* ...	1	0	12
With *fodiens* ...	1	0	6

TABLE XX.

Colour of male pygidium (seventh tergite) in *Epeolus cruciger*.

Specimens.	Red.	Part red.	Black.
All specimens ...	51	21	18
With *succincta* ...	2	5	7
With *marginata* ...	9	4	1
Other specimens ...	40	12	10

TABLE XXI.

Colour of the tibiae in *Epeolus variegatus* males.

Specimens.	Tibia.	Red.	Red with dark mark.	Mainly dark.
All specimens ...	I	58	38	10
	II	65	36	8
	III	54	48	7
With *marginata* ...	I	4	2	1
	II	4	2	1
	III	4	1	2
With *daviesana* ...	I	2	1	2
	II	2	1	2
	III	2	1	2
With *similis* ...	I	5	4	4
	II	4	6	3
	III	3	6	4
With *fodiens* ...	I	4	3	0
	II	5	2	0
	III	4	3	0

TABLE XXII.

Colour of the tibiae in *Epeolus cruciger* males.

Specimens.	Tibia.	Red.	Red with dark mark.
All specimens ...	I	69 ...	22
	II	70 ...	21
	III	70 ...	21
With *succincta* ...	I	10 ...	4
	II	11 ...	3
	III	11 ...	3
With *marginata* ...	I	10 ...	5
	II	10 ...	5
	III	9 ...	6
Other specimens ...	I	49 ...	13
	II	49 ...	13
	III	50 ...	12

Table XXIII.

Colour of the mid and hind femora in *Epeolus variegatus* females.

Specimens.	Mid femora.			Hind femora.		
	I.	II.	III.	I.	II.	III.
All specimens ...	76	191	6	172	91	10
With *marginata* ...	2	8	0	6	4	0
With *daviesana* ...	12	15	0	18	9	0
With *similis* ...	12	15	1	21	7	0
With *fodiens* ...	7	25	0	25	7	0

Note. — I = black or mainly black; II = red with large dark mark; III = red or mainly red. *Fodiens* parasites differ significantly in the mid femora from both *daviesana* and *similis* parasites (P. lies between ·05 and ·02).

Table XXIV.

Colour of the mid and hind femora in *Epeolus cruciger* males.

Specimens.	Mid femora.			Hind femora.		
	I.	II.	III.	I.	II.	III.
All specimens ...	41	49	1	9	70	12
With *succincta* ...	5	8	1	1	12	1
With *marginata* ...	9	6	0	0	15	0
Other specimens ...	27	35	0	8	43	11

Note. — I = black or mainly black; II = red with large dark mark; III = red or mainly red.

Table XXV.

Colour of hind coxae beneath in *Epeolus cruciger* females.

Specimens.	Mainly black.	Half red.	Mainly red.
All specimens ...	96	123	80
With *succincta* ...	23	26	8
With *marginata* ...	16	11	9
Other specimens ...	57	86	63

Table XXVI.

Number of hamuli on the hindwings of *Epeolus variegatus*.

Specimens.	Sex.	9.	10.	11.	12.	13.	14.	15.	Mean.
All specimens ...	♀	1	6	63	109	69	24	1	12·15
	♂	4	21	39	30	8	6	1	11·36
With *marginata* .	♀	0	1	2	3	4	0	0	12·00
	♂	1	2	2	2	0	0	0	10·70
With *daviesana* ..	♀	1	1	10	10	4	1	0	11·66
	♂	0	1	1	2	1	0	0	11·60
With *similis* ...	♀	0	0	5	13	5	5	0	12·60
	♂	1	2	4	3	2	1	0	11·50
With *fodiens* ...	♀	0	0	8	14	9	1	0	12·10
	♂	1	2	2	2	0	0	0	10·70

Table XXVII.

Number of hamuli on the hindwings of *Epeolus cruciger*.

Specimens.	Sex.	9.	10.	11.	12.	13.	Mean.
All specimens ...	♀	13	109	130	53	8	10·79
	♂	14	43	22	11	1	10·36
With *succincta* ...	♀	2	14	27	12	2	10·96
	♂	0	9	3	2	0	10·50
With *marginata* ...	♀	3	13	16	3	1	10·61
	♂	7	4	3	1	0	9·87
Other specimens ...	♀	8	82	87	38	5	10·77
	♂	7	30	16	8	1	10·45

Table XXVIII.

Length of body of *Epeolus cruciger* (in millimetres).

Specimens.	Sex.	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	Mean.
All specimens ..	♀	0	3	16	43	72	68	64	32	12	2	7·63
	♂	1	5	9	20	18	24	11	2	1	0	7·00
With *succincta*	♀	0	0	2	4	4	5	23	13	4	1	7·91
	♂	0	0	1	0	2	6	4	1	0	0	7·54
With *marginata*	♀	0	0	4	17	8	6	1	0	0	0	6·76
	♂	1	2	3	7	0	1	1	0	0	0	6·33
Other specimens	♀	0	3	10	22	60	57	40	19	8	1	
	♂	0	3	5	13	16	18	6	1	1	0	

Note. When males or females of *marginata* and *succincta* parasites are compared, the value of P is less than ·01.

Table XXIX.

Length of body of *Epeolus variegatus* (in millimetres).

Specimens.	Sex.	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10	Mean.
All specimens	♀	0	0	2	11	35	74	72	48	18	10	1	2	7·40
	♂	1	3	9	25	34	21	11	5	0	0	0	0	6·51
With														
marginata	♀	0	0	1	3	2	3	0	1	0	0	0	0	6·55
	♂	1	1	0	2	2	1	0	0	0	0	0	0	5·93
daviesana	♀	0	0	1	3	4	9	8	2	0	0	0	0	6·98
	♂	0	0	0	2	1	0	2	0	0	0	0	0	6·70
similis ...	♀	0	0	0	2	1	7	6	7	4	1	0	0	7·55
	♂	0	0	0	2	5	5	1	0	0	0	0	0	6·70
fodiens ...	♀	0	0	0	2	5	10	10	1	1	2	0	1	7·31
	♂	0	0	0	1	2	2	1	1	0	0	0	0	6·93

Note. In the females the following comparisons are significant :—*Marginata* parasites compared with *daviesana* (P between ·02 and ·01), with *similis* (P less *than* ·01), with *fodiens* (P between ·02 and ·01). *Daviesana* parasites compared with *similis* (P less than ·01).

In the males the following comparisons are significant :—*Marginata* parasites compared with *similis* (P between ·02 and ·01), with *fodiens* (P between ·05 and ·02).

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